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ORIGINAL PAPER

# Growth and photosynthetic responses of *Fraxinus mandshurica* seedlings to various light environments

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**Abstract:** To determine light requirement and adaptability of *Fraxinus mandshurica* seedlings, the seasonal variations of photosynthetic variables were measured in 3-year-old seedlings grown under four light levels (100%, 60%, 30%, and 15% of full sunlight) with a LI-6400 portable photosynthesis system. The leaf chlorophyll content, special leaf weight, annual height and basal diameter increment of seedlings were also observed. The maximum and minimum values of net photosynthetic rate, maximum rate of carboxylation, and maximum rate of electron transport of *F. mandshurica* seedlings were detected with 60% and 15% of full sunlight treatments, respectively. With the decrease of light level, both light saturation point and special leaf weight significantly declined ($p < 0.05$), but leaf chlorophyll content significantly increased ($p < 0.05$). Annual height and basal diameter increments of seedlings grown under 60% of full sunlight treatment were significantly greater than those of seedlings under other treatments ($p < 0.05$). It was concluded that *F. mandshurica* seedlings can adapt to a wide range of light environments from 15% to 100% of full sunlight by adjusting light saturation point, leaf chlorophyll content and special leaf weight. According to the maximum of relative growth, 60% of full sunlight treatment is the optimum light level for the growth of 3-year-old *F. mandshurica* seedlings.

**Keywords**: *Fraxinus mandshurica*; light adaptation; plasticity; seasonal dynamics; secondary forest

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## Introduction

*Fraxinus mandshurica* is a major tree species with high ecological and economical values in the mixed broadleaved-Korean pine (*Pinus koraiensis* Sieb. Et Zucc) forests in Northeast China. However, after more than a century of anthropogenic disturbances, e.g., timber exploitation, *F. mandshurica* resource has greatly declined (Chen et al. 2002; Zhu et al. 2007). Thus, it has been put on the list of vulnerable and national protection tree species (Wang et al. 1994). In recent years, the decline of *F. mandshurica* resource has been paid a wide attention (Newton et al. 1999), and a lot of efforts have been made to preserve and restore *F. mandshurica* forests (Ding et al. 1991; Yamamoto et al. 1995; Utsumi et al. 1999). Light plays a vital role in survival and growth of many forest trees underneath the canopy (Modrý et al. 2004). Especially in the secondary forests, light is one of the most important environmental factors in the processes of their natural regeneration (Zhu et al. 2003). Since light environments vary greatly during the growth and development of forests at both temporal and spatial scales, the seed germination, survival and distribution of seedlings are determined by the light adaptability (Messier & Bellefleur 1988). Studies revealed that there were more *F. mandshurica* seedlings in the gap than underneath the canopy. The number of 1-year-old seedlings was significantly more than that of older ones (Zang et al. 1999; Han et al. 2004). Wang et al. (2006) found that most of *F. mandshurica* seedlings died off in the 3rd year, and only 2% of the emerging seedlings survived under forests in Changbai Mountains. There are significantly positive correlations between survival and growth of seedlings and light levels (McGuire et al. 2001). However, there is little information on the quantitative analysis of the suitable light level for *F. mandshurica* seedlings growth.

In this study, several photosynthetic variables (including maximum net photosynthetic rate, dark respiration rate, light compensation point, light saturation point, maximum rate of carboxylation, and maximum rate of electron transport) were susceptible to changes in sunlight, and other morphological and

physiological parameters (e.g., leaf chlorophyll content, special leaf weight, increment of annual height and basal diameter) of 3-year-old seedlings of *F. mandshurica* grown under 15%, 30%, 60% and 100% of full sunlight were investigated. The study aims at determining the optimum light level for 3-year-old seedlings of *F. mandshurica* in different light levels.

## Materials and methods

### Study area

The study site is located at the Qingyuan Experimental Station of Forest Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, in Qingyuan County, a mountainous region in eastern Liaoning Province, northeastern China (41º51'6.1"–41º51'16.5"N, 124º54'32.6"–124º54'48.2"E, at 500–1100 m above sea level). The climate is a continental monsoon climate, with strong spring winds, a warm humid summer and a dry cold winter. The annual mean air temperature is 4.7°C with the maximum low temperature of -37.6°C and the maximum high temperature 36.5°C. Annual mean precipitation is 810.9 mm. The frost-free period is 130 days, with first frost in October and last frost in April. The forest species in study site mainly contains *Quercus mongolica*, *Juglans mandishurica*, *F. mandishurica*, *Phellodendron amurense*, *Acer mono*, *Pinus koraensis*, *Larix* spp., *Betula* spp., and *Tilia* spp. in the tree layer (Zhu et al. 2008).

### Experimental design and treatments

Forty even-sized *F. mandshurica* seedlings (2-years-old) were randomly planted in four plots in May 2007. Each plot was 15 m × 2 m in dimension and contained top-layer forest soil to 1-m depth. Light treatments were designed in four levels as full sunlight (FI, 100% of full sunlight), high sunlight (HI, 60% of full sunlight), moderate sunlight (MI, 30% of full sunlight) and low sunlight (LI, 15% of full sunlight). Shading treatment was achieved by suspending different layers of black nylon net above and surrounding each plot. The photosynthetic photon flux density (PPFD, 400-700 nm) with the four light treatments during the study period was measured at intervals of 10 s, and the 30-min averaged values were recorded from 5:00 to 18:00 (GMT+008) for continuous three sunny days each month from May to September in 2008, using four LI-191SA line quantum sensors attached to a LI-1400 data logger (Li-Cor, Lincoln, NE, USA). The light level in each treatment was calculated by comparing with the full sunlight (Fig. 1). There was enough space between each seedling (40 cm between each seedling) so that the seedlings could not be shaded each other. They were watered except the rainy season, and each treatment got equivalent water in order that water was not the limiting factor during the experiment. Weeding and diseases/pests control were conducted during the growing season. Measurement was done from May to September in 2008.

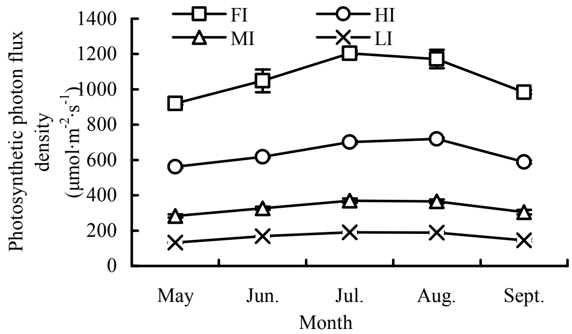


**Fig. 1 Average photosynthetic photon flux density in four light intensity treatments (Wang et al. 2010)**

FI is Full irradiance; HI is High irradiance; MI is Moderate irradiance; LI is Low irradiance.

### Photosynthetic measurements

The photosynthetic parameters of healthy and upper-crown sun-facing leaves were measured by a portable computerized open gas system IRGA (LI-6400, LiCor, Lincoln, NE, USA). The photosynthetic light response curves were developed by measuring photosynthetic rate at 11 levels of PPFD (i.e., 0, 20, 50, 100, 200, 400, 600, 800, 1000, 1500 and 2000 μmol·m$^{-2}$·s$^{-1}$) under ambient $CO_2$ concentration of 380 μmol·mol$^{-1}$. Measurements were repeated on three leaves from three different seedlings for each treatment. The photosynthetic variables were obtained by fitting the photosynthetic light response curve (Farquhar et al. 2001) including maximum net photosynthetic rate ($P_{\max}$), dark respiration rate ($R_d$), light compensation point (LCP) and light saturation point (LSP).

$$P_n = \frac{\Phi * P_{PFD} + P_{\max} - \sqrt{(\Phi * P_{PFD} + P_{\max})^2 - 4 * \Phi * P_{PFD} * K * P_{\max}}}{2 * K} - R_d \quad (1)$$

where, $P_n$ (μmol·m$^{-2}$·s$^{-1}$) is the net photosynthetic rate, $P_{PFD}$ (μmol·m$^{-2}$·s$^{-1}$) the photosynthetic photon flux density, $P_{\max}$ (μmol·m$^{-2}$·s$^{-1}$) the maximum net photosynthetic rate. $\Phi$ (mol·mol$^{-1}$) the apparent quantum yield. $K$ the curved angle in the photosynthetic light response curve, and $R_d$ (μmol·m$^{-2}$·s$^{-1}$) is the dark respiration rate.

The curves of photosynthetic response to intercellular $CO_2$ concentration ($A/C_i$) were developed by measuring the rate of photosynthesis at 10 $CO_2$ concentrations, beginning with 400 μmol·mol$^{-1}$, then 300, 200, 100, 50, 400, 600, 800, 1000 and 1500 μmol·mol$^{-1}$, at saturated PPFD with artificial LI-6400-02B light source. During measurements, temperature and relative humidity in the chamber were set at 25°C and at 50% respectively. Maximum rate of carboxylation ($V_{c\max}$) and maximum rate of electron transport ($J_{\max}$) were estimated from the $A/C_i$ curves fit by nonlinear regression based on the model of Farquhar et al. (1980).

$$A_c = \frac{V_{c\max}(C_i - \Gamma^*)}{C_i + K_c(1 + O/K_o)} - R_d \quad (2)$$

where, $A_c$ (μmol·m$^{-2}$·s$^{-1}$) is the photosynthetic rate limited by Rubisco activity, $C_i$ (μmol·mol$^{-1}$) is the intercellular $CO_2$ concentration, $\Gamma^*$ (μmol·mol$^{-1}$) is the $CO_2$ compensation point, $K_c$ and $K_o$ are Michaelis-Menten constants of Rubisco activity for $CO_2$ and $O_2$, respectively. $\Gamma^*$ = 42.8 μmol·mol$^{-1}$, $K_c$ = 405 μmol·mol$^{-1}$, $K_o$ = 278 mmol·mol$^{-1}$, $R_d$ = 0.02*$V_{cmax}$ (Bernacchi et al. 2001).

$J_{max}$ was calculated by fitting the following equation (Farquhar et al. 1980) to a near-plateau of A/$C_i$ curves ($C_i$ > 600 μmol·mol$^{-1}$):

$$A_j = \frac{J_{\max}(C_i - \Gamma^*)}{4C_i + 8\Gamma^*} - R_d \quad (3)$$

where, $A_j$ (μmol·m$^{-2}$·s$^{-1}$) is the photosynthetic rate limited by RuBP regeneration, and $C_i$ is the $CO_2$ concentration at which photosynthesis was co-limited by RuBP carboxylation. RuBP regeneration and was calculated from equations 2 and 3 with $A_c$ = $A_j$.

Leaf chlorophyll content and special leaf weight

Leaves used in gas exchange measurements were picked up and immediately pictured to determine their surface area by Photoshop (7.0) software (Adobe Inc.). Then they were dried at 80°C to constant weight for determining the special leaf weight (SLW). Leaf chlorophyll (Chl) content was determined pectrophotometically in 80% acetone extracts according to Li (2000).

Growth measurement

In early and late growth period of 2008, 10 seedlings from each plot were selected for height and basal diameter measurement. The increment of annual height and basal diameter of seedlings was determined by the difference of values between final and initial heights and basal diameters in 2008.

Statistical analysis

Differences in the effects of different light levels on the growth and photosynthesis of *F. mandshurica* seedlings in different seasons were analyzed by one-way ANOVA. Differences were considered significant at $p < 0.05$. All statistical tests were performed using SPSS 13.0 (SPSS Inc.).

## Results

Seasonal variations in photosynthetic variables

During all the growing season, $P_n$ increased rapidly with increasing photosynthetic photon flux density (PPFD) when PPFD was lower than 400 μmol·m$^{-2}$·s$^{-1}$, and the value increased slowly then kept constant with the continuing increasing of PPFD (Fig. 2). In both spring and autumn, $P_{max}$ was lower in LI treatment than that in the other treatments ($p < 0.05$, Table 1), but there were no significant differences in $P_{max}$ across light levels in summer ($p > 0.05$). $R_d$ was greater in summer than that in autumn ( $p < 0.05$), but did not differ across the light irradiances ($p > 0.05$, Table 1).

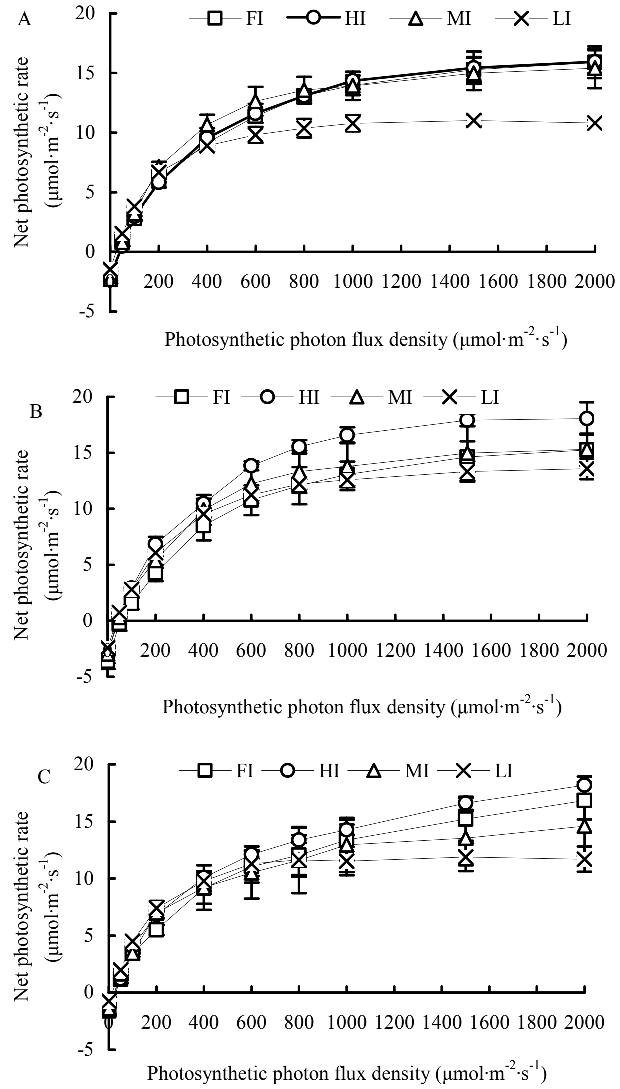


**Fig. 2 Responses of $P_n$ to PPFD in *F. mandshurica* seedlings under the four light levels in spring (A), summer (B) and autumn (C).**
FI is Full irradiance; HI is High irradiance; MI is Moderate irradiance; LI is Low irradiance.

LCP in FI treatment was higher than that in LI treatment in summer and autumn, and the value was greater in spring and summer than that in autumn ($p < 0.05$). LSP increased with the increasing light levels ($p < 0.05$), but did not display significantly seasonal changes ($p > 0.05$, Table 1). $V_{cmax}$ increased with the increase of light levels in spring, but the value in HI treatment was greater than that in the other light treatments in summer ($p < 0.05$). There was no significant difference in $J_{max}$ among the light levels in spring ($p > 0.05$), but the value was

greater in HI treatment than that in the other treatments in summer ( $p < 0.05$, Table 1).

**Table 1. Photosynthetic parameters of *F. mandshurica* seedlings under 4 light levels in spring, summer and autumn (Means±SE, n=3, $p < 0.05$)**

| Photosynthetic variables | Light levels | Spring | Summer | Autumn |
|---|---|---|---|---|
| Maximum net photosynthetic rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | FI | 15.90±1.33bA | 15.27±1.45aA | 16.83±1.64bA |
| | HI | 16.04±1.07bA | 18.07±1.44aA | 18.17±0.77bA |
| | MI | 15.43±1.62bA | 15.43±2.68aA | 14.59±2.62abA |
| | LI | 11.10±0.44aA | 13.70±0.92aA | 11.87±1.21aA |
| Dark respiration rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | FI | 2.24±0.39aAB | 3.64±0.67aB | 1.62±0.37aA |
| | HI | 2.00±0.41aAB | 2.99±0.79aB | 1.06±0.13aA |
| | MI | 2.30±0.37aAB | 2.96±0.15aB | 1.41±0.48aA |
| | LI | 1.49±0.19aA | 2.42±0.06aB | 0.73±0.34aA |
| Light compensation point ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | FI | 40.13±7.21aA | 64.47±10.75bB | 29.71±3.42bA |
| | HI | 40.05±5.58aB | 45.81±3.97abB | 22.51±0.53abA |
| | MI | 39.81±6.15aB | 49.49±3.45abB | 23.61±5.72abA |
| | LI | 25.58±2.48aB | 43.00±1.07aC | 12.68±4.26aA |
| Light saturation point ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | FI | 1533±33cA | 1533±33cA | 1633±67cA |
| | HI | 1267±145bcA | 1400±208bcA | 1433±120bcA |
| | MI | 1000±115abA | 1067±145abA | 1033±145abA |
| | LI | 800±115aA | 667±67aA | 800±200aA |
| Maximum rate of carboxylation ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | FI | 59.28±8.51bA | 55.24±1.40aA | 49.11±5.18abA |
| | HI | 49.68±4.22abA | 74.74±7.97bB | 58.26±4.91bAB |
| | MI | 42.90±2.90aA | 57.30±2.48aB | 57.47±1.67bB |
| | LI | 37.94±0.20aA | 53.55±2.10aB | 40.51±1.26aA |
| Maximum rate of electron transport ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | FI | 87.62±2.03aA | 80.18±10.81aA | 138.49±5.31bB |
| | HI | 84.73±5.72aA | 132.58±3.11bB | 132.51±7.70bB |
| | MI | 71.54±2.80aA | 100.00±6.02aB | 123.80±5.95bC |
| | LI | 65.76±14.6aA | 81.36±4.23aA | 87.30±4.24aA |

**Notes**: Different lowercase letters indicate significant differences ($p < 0.05$) among different light intensity treatments within the same season. Different capital letters indicate significant differences ($p < 0.05$) among different seasons. FI is Full irradiance; HI is High irradiance; MI is Moderate irradiance; LI is Low irradiance.

Seasonal variations in leaf chlorophyll content and special leaf weight

With decreasing light levels, leaf chlorophyll content significantly increased ($p < 0.05$, Fig. 3A) and special leaf weight (SLW) significantly declined ($p < 0.05$, Fig. 3B). SLW was lower in spring than that in summer and autumn ($p < 0.05$, Fig. 3B).

Growth differences

Annual height increment of *F. mandshurica* seedlings reached the maximum and the minimum in HI treatment and in LI treatment, respectively (Fig. 4A). Annual basal diameter increment for the seedlings grown in HI treatment was greater than that in other light levels ($p < 0.05$, Fig. 4B).

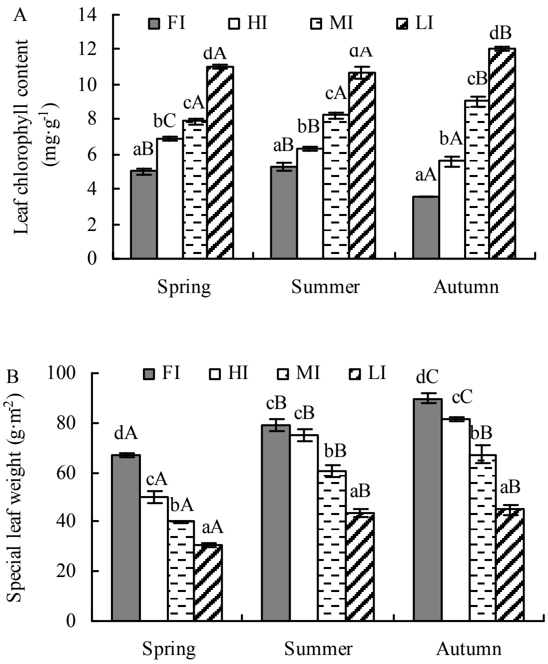


**Fig. 3 Leaf chlorophyll content (A) and special leaf weight (B) of leaves of *F. mandshurica* seedlings under the four light intensity treatments in spring, summer and autumn (Means±SE; n=3, *P*<0.05).** FI is Full irradiance; HI is High irradiance; MI is Moderate irradiance; LI is Low irradiance.

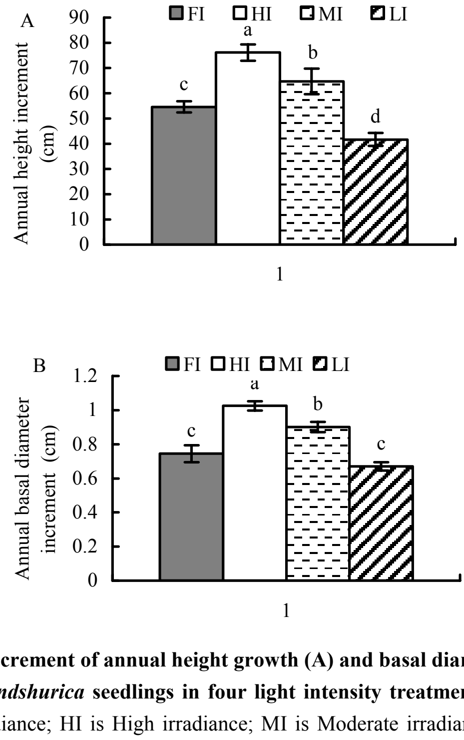


**Fig. 4 Increment of annual height growth (A) and basal diameter (B) of *F. mandshurica* seedlings in four light intensity treatments.** FI is Full irradiance; HI is High irradiance; MI is Moderate irradiance; LI is Low irradiance.

## Discussion and conclusions

Photosynthesis is one of the most important physiological parameters affecting the growth of forest trees, and its seasonal variation determined the carbon balance and the relationship of carbon metabolism and material production (Kramer & Kozlowski 1979). There was no significantly seasonal change in $P_{max}$ of *F. mandshurica* seedlings, but its $R_d$ was greater in summer than that in autumn, indicating that most of photosynthetic products in summer were consumed by respiration. Under low light conditions, some forest trees adopt a strategy of energy conservation, i.e., minimizing $CO_2$ loss through respiration and producing a positive carbon balance, to survive and grow (Björkman 1981). $R_d$ and LCP significantly declined in autumn, which contributed to effectively using weak light to increase carbon accumulation for seedling growth. LCP and LSP were effective indicators of light requirements of plants, and sciophytes generally exhibited lower values than heliophytes (Larcher 2003). LCP of *F. mandshurica* seedlings under different light levels during the growing season varied from 12.68 to 64.47 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which was between sciophyte (LCP < 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and heliophyte (LCP > 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$), (Xia et al. 2008). LSP of *F. mandshurica* seedlings increased with the increasing of light level, indicating the good adaptability and plasticity in changes of light regimes.

Light has a remarkable effect on leaf pigment composition. The variation in chloroplast composition in response to varying light regimes could lead to successful acclimation of tree growth to light environments (Duan et al. 2005). Chlorophyll content would decline when the trees were exposed to excess light due to a breakdown of the structural integrity of chloroplasts (Rhizopoulou et al. 1991). Leaf chlorophyll content of *F. mandshurica* seedlings increased with the decrease of light levels (Fig. 3A), this may be because the seedlings would enhance the light harvesting capacity in low light condition by increasing chlorophyll content. There were closely positive correlations between special leaf weight and light level (Rosati et al. 2001). Through the special leaf weight decreased, plants would increase leaf area and improve light harvesting capacity under low light environments (Lambers & Poorter 1992), which could be beneficial to the increase of carbon accumulation (Kitao et al. 2000). Special leaf weight of *F. mandshurica* seedlings declined with the decreasing of light levels (Fig. 3B), which could prevent against photoinhibition under higher irradiance and enhance the ability of capturing light under lower irradiance (Bloor 2003). These results indicated that *F. mandshurica* seedlings could adapt to a wide range of light environments, thus they can regenerate not only under full natural light but also underneath the canopy, in agreement with the findings of Zhao et al. (1991).

Generally, values of maximum net photosynthetic rate, maximum rate of carboxylation and maximum rate of electron transport in seedlings grown in HI treatment were greater than those in other treatments. Sang et al. (1999) found that due to photoinhibition, the seedlings showed midday depression under full natural light. These findings above could explain the case that the increment of annual height and basal diameter of *F. mandshurica* seedlings was greater in HI and MI treatments than that in FI and LI treatments. Thus, appropriate shading (60% of full sunlight) should be better for the growth of the 3-year-old *F. mandshurica* seedlings, which was consistent with some other studies in which growth of seedlings was greater at canopy density of 0.5 than full natural light and canopy density of 0.7 (Wang et al. 2006). However, excessive shade (15% of full sunlight) would severely inhibit growth of *F. mandshurica* seedlings. The values of maximum net photosynthetic rate, maximum rate of carboxylation and maximum rate of electron transport for seedlings grown in LI treatment were lowest among all the treatments, which may induce the failure of the seedling survival in the low light levels (less than 15% of full sunlight); this was because low photosynthetic rate caused carbon imbalance between carbon metabolism and material production.

In conclusion, *F. mandshurica* seedlings can adapt to a wide range of light environments by adjusting light saturation point, leaf chlorophyll content and special leaf weight. According to the maximum of relative growth, 60% of full sunlight is the optimum light level for the growth of *F. mandshurica* seedlings in the 3rd year. For the regeneration of *F. mandshurica*, the microsites in forest edge and gaps should be favored to provide an adequate light environment to ensure greater survival rate and faster initial growth of seedlings.

## References

Bernacchi CJ, Singsaas EL, Pimentel C, Portis AR, Long SP. 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant, Cell & Environment*, **24**: 253−259.

Björkman O. 1981. Responses to different quantum flux densities. In: O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler (eds). *Encyclopedia of Plant Physiology*. New Series, Vol 12A. New York: Springer, Berlin Heidelberg, pp. 57−107.

Bloor JMG. 2003. Light responses of shade-tolerant tropical tree species in north-east Queensland: a comparison of forest- and shadehouse-grown seedlings. *Journal of Tropical Ecology*, **19**: 163−170.

Chen XW, Zhou GS, Zhang XS. 2002. Spatial characteristics and change for tree species along the North East China Transect (NECT). *Plant Ecology*, **164**: 65−74.

Ding Baoyong, Shen Hailong, Liu Qiang, Wang Lu. 1991. Preliminary studies on the characters of growth and development and the method of tending thinning for Manchurian ash natural secondary forest. *Journal of Northeast Forestry University*, **19**(4): 147−155. (in Chinese)

Duan BL, Lu YW, Yin CY, Li CY. 2005. Morphological and physiological plasticity of woody plant in response to high light and low light. *Chinese Journal of Applied & Environmental Biology*, **11**(2): 238−245.

Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic $CO_2$ assimilation in leaves of $C_3$ species. *Planta*, **149**: 78−90.

Farquhar GD, von Caemmerer S, Berry JA. 2001. Models of photosynthesis. *Plant Physiology*, **125**: 42−45.

Han Youzhi, Wang Zhengquang, Gu Jiacun. 2004. The effects of spatial heterogeneity of understorey light availability on regeneration of Manchu-

rian ash. *Chinese Journal of Plant Ecology*, **28**(4): 468−475. (in Chinese)

Kitao M, Lei TT, Koike T, Tobita H, Maruyama Y. 2000. Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. *Plant, Cell & Environment*, **23**: 81−89.

Kramer PJ, Kozlowski TT. 1979. Physiology of Woody Plants. New York: Academic Press, p. 811.

Lambers H, Poorter H. 1992. Inherent variation in growth-rate between higher-plants－a search for physiological causes and ecological consequences. In: M. Begon, A.H. Fitter (eds), *Advances in Ecological Research*. London: Academic Press, pp. 187−261.

Larcher W. 2003. Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups. Germany: Springer Verlag, p. 513.

Li Hesheng. 2000. The Experiment Principle and Technique for Plant Physiology and Biochemistry. Beijing: Higher Education Press, pp. 134−138. (in Chinese)

McGuire JP, Mitchell RJ, Moser EB, Pecot SD, Gjerstad DH, Hedman CW. 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understorey response to tree removal in longleaf pine savannas. *Canadian Journal of Forest Research*, **31**: 765−778.

Messier C, Bellefleur P. 1988. Light quantity and quality on the forest floor of pioneer and climax stages in a birch - beech - sugar maple stand. *Canadian Journal of Forest Research*, **18**: 615−622.

Modrý M, Hubený D, Rejšek K. 2004. Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. *Forest Ecology and Management*, **188**: 185−195

Newton AC, Allnutt TR, Gillies ACM, Lowe AJ, Ennos RA. 1999. Molecular phylogeography, intraspecific variation and the conservation of tree species. *Trends in Ecology and Evolution*, **14**: 140−145.

Rhizopoulou S, Meletiouchristou MS, Diamantoglou S. 1991. Water relations for sun and shade leaves of four Mediterranean evergreen sclerphylls. *Journal of Experimental Botany*, **42**: 627−635.

Rosati A, Badeck FW, Dejong TM. 2001. Estimating canopy light interception and absorption using leaf mass per unit leaf area in *Solanum melongena*. *Annals of Botany*, **88**: 101−109.

Sang Yunrong, Wang Chuankuan, Lang Guanglin, Zhou Xiaofeng, Zhao Huixun. 1999. Photosynthetic efficiency of *Fraxinus mandshurica*. *Journal of Northeast Forestry University*, **27**(2): 15−18. (in Chinese)

Utsumi Y, Sano Y, Funada R, Fujikawa S, Ohtani J. 1999. The progression of cavitation in earlywood vessels of *Fraxinus mandshurica* var *japonica* during freezing and thawing. *Plant Physiology*, **121:** 897–904.

Wang Guangfa, Zhuang Faming, Zhao Junchang. 2006. Artificial regeneration of *Fraxinus mandshurica* forest range of Changbai Maintain. *Jinlin Forestry Science and Technology*, **35**(3): 13−18. (in Chinese)

Wang Kai, Zhu Jiaojun, Yu Lizhong, Sun Yirong, Zhang Jinxin. 2010. Effects of light environment on Juglans mandshurica seedlings growth and photosynthesis. *Chinese Journal of Applied Ecology*, **21**(4): 821−826. (in Chinese)

Wang Yihong, Chai Yixin, Mu Changlong. 1994. Study on ecology of *Fraxinus mandshurica*. *Journal of Northeast Forestry University*, **22**(1): 1-6. (in Chinese)

Xia Jiangbao, Zhang Guangcan, Liu Jingtao, Liu Qing, Chen Jian. 2008. Responses of photosynthetic and physiological parameters in *Campsis radicans* to soil moisture and light intensities. *Journal of Beijing Forestry University*, **30**(5): 13−18. (in Chinese)

Yamamoto F, Sakata T, Terazawa K. 1995. Physiological, morphological and anatomical responses of *Fraxinus mandshurica* seedlings to flooding. *Tree Physiology*, **15**: 713-719.

Zang Runguo, Xu Huacheng, Gao Wentao. 1999. Regeneration response of main tree species to gap size and gap development phase in the Korean pine-broadleaved forest in Jiaohe, Northeast China. *Scientia Silvae Sinicae*, **35**(3): 2−9. (in Chinese)

Zhao Huixun, Chai Yixin, Zhang Dongli. 1991. Photosynthesis determination on some tree species and the forest management suggestions. *Journal of Northeast Forestry University*, **19**: 284−289. (in Chinese)

Zhu JJ, Liu ZG, Wang HX, Yan QL, Fang HY, Hu LL, Yu LZ. 2008. Effects of site preparation on emergence and early establishment of *Larix olgensis* in montane regions of northeastern China. *New Forests*, **36**: 247−260.

Zhu JJ, Mao ZH, Hu LL, Zhang JX. 2007. Plant diversity of secondary forests in response to anthropogenic disturbance levels in montane regions of northeastern China. *Journal of Forest Research*, **12**: 403−416.

Zhu JJ, Matsuzaki T, Lee FQ, Gonda Y. 2003. Effect of gap size created by thinning on seeding emergency, survival and establishment in a coastal pine forest. *Forest Ecology and Management*, **182**: 339−354.